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Abstract

Knowledge of the contributions of different chromosome segments to the expression of quantitative traits is limited. Information on the relative importance of loci on different chromosome arms could be used to identify blocks of genes that might be useful for improving inbreds and their hybrid progeny. One suggested technique to evaluate the relative importance of different chromosome arms of maize (*Zea mays* L.) for trait expression has been the use of B-A translocations. The objective of our study was to measure the contributions of the 10L segments from the inbreds B55, CI187-2, Oh43, M14, and N25 to the total heterotic effect observed in the hybrid of W22 and the respective inbreds. Field studies were conducted that included three strains of W22, their crosses to B55, CI187-2, Oh43, N25, and M14; and their crosses to five W22 lines that carried a substitution from each of the five non-W22 lines for the distal 67% of the long arm of chromosome 10 (10L). Data were collected for 11 plant and ear traits. Significant differences ($P \leq 0.05$) were detected among the three strains of W22 and their crosses. The differences, however, did not show a consistent pattern among strains for the 11 traits. Significant midparent heterosis was detected for most traits in the hybrids of the normal and 10L segment lines for grain yield and components of yield. The percentage of midparent heterosis accounted for by the 10L segment ranged from 9.4 to 20.8% for yield. There were differences among traits for the effects of segment 10L on trait expression, with the greatest effect for tasselbranch number and the least for kernel weight. These studies suggest that the use of B-A translocations to analyze more chromosome segments may be informative and may make possible the combining of different segments for creating superior lines and hybrids.

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Contribution of the Long Arm of Chromosome 10 to the Total Heterosis Observed in Five Maize Hybrids

K. R. Lamkey,* A. R. Hallauer, and D. S. Robertson

ABSTRACT

Knowledge of the contributions of different chromosome segments to the expression of quantitative traits is limited. Information on the relative importance of loci on different chromosome arms could be used to identify blocks of genes that might be useful for improving inbreds and their hybrid progeny. One suggested technique to evaluate the relative importance of different chromosome arms of maize (*Zea mays* L.) for trait expression has been the use of B-A translocations. The objective of our study was to measure the contributions of the 10L segments from the inbreds B55, CI187-2, Oh43, M14, and N25 to the total heterotic effect observed in the hybrid of W22 and the respective inbreds. Field studies were conducted that included three strains of W22, their crosses to B55, CI187-2, Oh43, N25, and M14; and their crosses to five W22 lines that carried a substitution from each of the five non-W22 lines for the distal 67% of the long arm of chromosome 10 (10L). Data were collected for 11 plant and ear traits. Significant differences ($P \leq 0.05$) were detected among the three strains of W22 and their crosses. The differences, however, did not show a consistent pattern among strains for the 11 traits. Significant midparent heterosis was detected for most traits in the hybrids of the normal and 10L segment lines for grain yield and components of yield. The percentage of midparent heterosis accounted for by the 10L segment ranged from 9.4 to 20.8% for yield. There were differences among traits for the effects of segment 10L on trait expression, with the greatest effect for tassel-branch number and the least for kernel weight. These studies suggest that the use of B-A translocations to analyze more chromosome segments may be informative and may make possible the combining of different segments for creating superior lines and hybrids.

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ROBERTSON et al. (1981) presented the results of the first test of a technique using B-A translocations to transfer intact chromosome segments from one inbred line of maize to another (Robertson, 1964; 1967; Peterson and Wernsman, 1964). The technique involved transferring intact, the distal 67% of the long arm of chromosome 10 (10L) from four inbreds (i.e., B55, Oh43, CI187-2, and M14) into the inbred W22 background. Robertson et al. (1981) measured the effects of these chromosome 10L segments from different inbreds on performance as measured by 11 quantitative traits. In no instance did the substituted lines per se perform better than W22. Hybrids between different substituted lines were homozygous for most of the W22 genome, but heterozygous for the distal 67% of the long arm of chromosome 10 (e.g., B55, 10L/M14 10L, Oh43 10L/CI187-2 10L, etc.). Many of these hybrids performed better than W22 for some traits, but in no case did the hybrids exceed the best substituted parent line. Heterotic responses of the hybrids of the four substituted lines with the inbred W22 were observed in nine instances.

In the study reported by Robertson et al. (1981), the substituted lines were compared to and hybridized with W22(IA). They indicated that the use of W22(IA) complicated the interpretation of their results and could have biased the conclusions because two different strains of W22 were involved. The substituted lines have the background of W22 *R-scm2*, although they were crossed to W22(IA) to determine the effects of the 10L substituted segment.

We evaluated three strains of W22 per se [W22(IA), W22 *R-scm2*, and W22(WI)], in crosses with five normal, and five 10L substituted lines, and in crosses with

each other to determine if the background of W22 had an effect on the comparisons of Robertson et al. (1981). The objectives of our study were to: (i) determine if the results of the 1981 experiments were repeatable; (ii) determine if there were genetic differences among the three strains of W22; and (iii) measure the contributions of the 10L segments from the inbreds B55, CI187-2, Oh43, M14, and N25 to the total heterotic effect observed in the hybrid of W22 and the respective inbreds.

MATERIALS AND METHODS

The procedures for generating the substituted W22 *R-scm2* inbred lines were described by Robertson (1964, 1967) and Robertson et al. (1981). The stocks used in this study included three strains of W22, five inbred lines, and five substituted W22 *R-scm2* lines. The three strains of W22 were: W22(IA), an inbred line maintained by self pollination by Donald S. Robertson at Iowa State University; W22 *R-scm2*, a purple aleurone W22 line obtained from Jerry Kermicle, University of Wisconsin, and maintained at Iowa State University by self pollination; and W22(WI), a stock of W22 maintained at the University of Wisconsin and obtained from Jerry Kermicle. The five inbred lines were B55, CI187-2, Oh43, N25, and M14. Substituted W22 *R-scm2* lines that had the distal 67% of the long arm of chromosome 10 from the indicated inbred homozygous were B55 10L, CI187-2 10L, Oh43 10L, N25 10L, and M14 10L. The distal 67% of the long arm of chromosome 10 represents approximately 3% of the total length of the maize genome shown in the cytological map of maize chromosomes (Coe and Neuffer, 1977). The inbred lines (designated as normal lines to distinguish them from the substituted lines), W22 strains, and W22 strain crosses evaluated in this study are listed in Tables 1 and 2.

The 46 entries were evaluated in a randomized complete-block design with three replications. Three row plots, 5.38 m long with 0.76 m between rows, were used to eliminate competition effects between the inbreds and hybrids. Data were collected on the center row of each plot. All plots were overplanted and thinned to 18 plants per row (44 023 plants ha⁻¹). The experiment was grown at the Iowa State Agron-

omy and Agriculture Engineering Research Center near Ames for 3 yr (1982–1984 inclusive).

All plants in a plot were hand harvested, dried to a uniform moisture, and shelled to determine yield (Mg ha⁻¹). Kernel-row number, ear length (cm), ear diameter (cm), and cob diameter (cm) were calculated as the average of measurements on 10 randomly chosen ears per plot. Kernel depth (cm) was calculated as half the difference between ear and cob diameter. Stand was recorded approximately 4 wk after planting as the number of plants per plot. Days-to-silk was recorded as the number of days from planting to 50% silk emergence. Plant and ear height (cm) were calculated as the average of measurements on 10 competitive plants per plot and measured as the height from the ground to the node of the flag leaf (plant height) and the highest ear-bearing node (ear height). Tassel-branch number was determined as the average number of primary tassel branches on 10 competitive plants per row. Kernel weight (g) was recorded as the weight of 1000 kernels randomly sampled from each plot after shelling. Data from only one experiment (1982) were available for kernel weight.

Analyses of variance for a randomized complete-block design were computed for each experiment and combined across experiments (years). All effects in the model were considered fixed except years and replications. The LSD at the 5% significance level was calculated when the entry mean square was significant.

Midparent (MP) heterosis, calculated as the F₁ mean minus the average of the two parents, was tested for being significantly different from zero by using *t*-tests. The standard error of MP heterosis was calculated as the square root of 1.5 times the variance of an entry mean. The percentage of the total MP heterosis due to the 10L chromosome arm was calculated as 100 times the ratio of the MP heterosis in the 10L substituted line × W22 *R-scm2* hybrid and the MP heterosis in the corresponding normal line × W22 *R-scm2* hybrid.

RESULTS AND DISCUSSION

Environmental conditions were excellent for maize production in 1982 and 1984, and average in 1983. Mean grain yields were 4.83, 3.57, and 4.57 Mg ha⁻¹ in 1982, 1983, and 1984, respectively. The mean grain

Table 1. Means for yield and other agronomic traits averaged over 3 yr for inbred lines and W22 strain hybrids.

Genotype	Grain yield Mg ha ⁻¹	Kernel rows no.	Ear length cm	Diameter		Kernel depth cm	Height		Days to silk	Tassel branches no.	Kernel weight† g
				Ear	Cob		Plant	Ear			
W22(IA)	2.29	15.5	14.2	3.8	2.5	0.63	146	56	94.3	12.0	243.3
W22(WI)	2.37	16.0	14.4	3.7	2.5	0.58	146	57	95.3	15.6	198.7
W22 <i>R-scm2</i>	2.59	15.6	14.2	3.6	2.4	0.59	149	63	93.9	10.7	226.3
B55	3.83	16.5	18.3	4.2	2.9	0.64	173	76	93.4	12.8	234.3
CI187-2	2.77	13.8	14.9	3.6	2.6	0.48	159	79	99.0	9.5	182.0
M14	2.57	16.4	14.5	4.0	2.7	0.61	127	47	91.7	5.2	204.0
N25	2.95	15.8	17.3	4.3	3.0	0.64	162	76	93.2	10.0	237.3
Oh43	2.46	14.5	14.4	3.9	2.7	0.58	116	48	92.8	7.7	246.0
B55 10L	2.73	14.8	13.9	3.5	2.5	0.49	141	51	93.0	9.0	219.7
CI187-2 10L	1.09	14.7	13.3	3.5	2.6	0.46	147	56	97.2	9.3	217.0
M14 10L	2.37	17.6	15.2	3.6	2.6	0.54	138	53	95.4	15.8	198.7
N25 10L	1.61	15.0	13.1	3.5	2.3	0.57	138	49	95.6	10.7	243.3
Oh43 10L	2.75	15.2	14.6	3.6	2.5	0.57	125	42	93.8	11.0	189.7
W22(IA) × W22(WI)	3.25	16.5	15.2	3.9	2.6	0.66	163	63	93.3	16.3	229.3
W22(IA) × W22 <i>R-scm2</i>	3.40	16.3	15.8	3.9	2.6	0.66	162	70	93.2	14.5	225.0
W22(WI) × W22 <i>R-scm2</i>	2.91	16.2	14.8	3.7	2.5	0.60	149	63	93.7	18.1	210.7
LSD (0.05)	0.74	0.9	1.6	0.3	0.1	0.11	13	9	1.8	2.6	20.0

† Values are averages for 1 yr.

yield and coefficient of variation, averaged over environments, were 4.32 Mg ha⁻¹ and 15.3%, respectively.

There were significant differences ($P \leq 0.05$) among genotypes for all traits evaluated. The genotype \times year interaction was significant for all traits except ear length, cob diameter, and kernel depth.

Comparison of W22 Inbred Strains

The strains of W22 [W22(IA), W22(WI), and W22 *R-scm2*] per se performed similarly, although W22(WI) had significantly more tassel branches and smaller seeds than the other two (Table 1). Differences among the means of W22 strains averaged over hybrids with the five normal lines were significant for plant height, days-to-silk, tassel-branch number, and kernel weight (Table 2). For means over hybrids with the 10L substituted lines, there were significant differences among W22 strains for yield, days-to-silk, tassel-branch number, and kernel weight. Differences among the W22 strain means for most traits did not show a pattern, although W22(IA) was usually significantly different from either W22(WI) or W22 *R-scm2*. The interaction between W22 strains and the normal or 10L substituted

lines was not significant for any of the traits indicating that the performance of the W22 strains was not dependent on the normal or 10L substituted lines.

Perhaps the best method of evaluating differences among strains of W22 for quantitative traits is to compare the midparent (MP) heterosis observed in the three possible crosses among the W22 strains. MP heterosis for the hybrid W22(IA) \times W22(WI) was significant for all traits except ear length, ear diameter, kernel depth, ear height, days-to-silk, and kernel weight (Table 3). The hybrid W22(IA) \times W22 *R-scm2* showed significant MP heterosis for all traits except kernel depth, days-to-silk, and kernel weight. In contrast, MP heterosis for the hybrid W22(WI) \times W22 *R-scm2* was significant only for cob diameter and tassel-branch number. These data indicate that as pairs, W22(WI) and W22 *R-scm2* were more alike genotypically than either W22(IA) and W22(WI) or W22(IA) and W22 *R-scm2*.

This observation was further supported by a comparison of the performance of the strain crosses with the performance of the strains per se (Table 1). If there were no genetic differences among the strains of W22, the strain hybrids and the strains per se would be ex-

Table 2. Means for yield and other agronomic traits averaged over 3 yr for the hybrids of the W22 strains with the normal and 10L substituted lines.

Genotype	Grain yield Mg ha ⁻¹	Kernel rows no.	Ear length	Diameter		Kernel depth cm	Height		Days to silk	Tassel branches no.	Kernel weight† g
				Ear	Cob		Plant	Ear			
W22(IA) \times B55	8.62	16.4	19.3	4.3	2.9	0.73	220	100	89.9	18.2	302.0
W22(IA) \times CI187-2	7.89	16.7	21.2	4.6	2.9	0.83	224	112	90.0	13.6	284.3
W22(IA) \times M14	6.79	18.0	20.7	4.5	2.8	0.83	195	83	89.0	13.2	241.0
W22(IA) \times N25	7.16	16.5	20.0	4.7	3.0	0.86	216	100	89.4	17.0	301.7
W22(IA) \times Oh43	7.06	15.8	17.8	4.5	2.7	0.88	191	79	87.1	13.6	292.3
Mean	7.50	16.7	19.8	4.5	2.9	0.83	209	95	89.1	15.1	284.3
W22(WI) \times B55	8.46	16.6	21.3	4.6	2.8	0.88	212	98	89.1	20.2	277.0
W22(WI) \times CI187-2	7.49	17.0	20.9	4.5	2.9	0.81	221	110	89.8	17.5	259.7
W22(WI) \times M14	6.49	18.3	19.8	4.4	2.8	0.82	196	89	89.8	15.5	235.0
W22(WI) \times N25	7.79	16.9	19.9	4.7	3.1	0.84	218	101	89.7	19.6	294.3
W22(WI) \times Oh43	6.33	16.3	19.9	4.5	2.7	0.87	186	76	88.4	14.8	289.0
Mean	7.31	17.0	20.4	4.5	2.9	0.84	207	95	89.4	17.5	271.0
W22 <i>R-scm2</i> \times B55	7.99	16.5	21.1	4.5	2.8	0.86	206	96	88.3	18.9	294.3
W22 <i>R-scm2</i> \times CI187-2	7.73	16.5	20.4	4.4	2.8	0.82	216	112	89.4	14.7	250.7
W22 <i>R-scm2</i> \times M14	6.40	17.8	20.5	4.4	2.7	0.83	188	88	89.0	14.2	236.7
W22 <i>R-scm2</i> \times N25	7.87	16.6	19.9	4.5	3.0	0.76	208	95	88.2	19.8	278.3
W22 <i>R-scm2</i> \times Oh43	7.20	16.4	19.7	4.4	2.7	0.85	186	76	86.8	15.4	292.3
Mean	7.44	16.8	20.3	4.4	2.8	0.82	201	93	88.3	16.6	270.5
W22(IA) \times B55 10L	3.66	15.7	15.0	3.8	2.5	0.66	156	59	92.2	12.1	239.7
W22(IA) \times CI187-2 10L	2.39	15.7	13.9	3.8	2.5	0.62	149	57	94.0	11.6	233.0
W22(IA) \times M14 10L	3.12	16.8	15.1	3.9	2.6	0.65	152	57	93.2	15.5	226.0
W22(IA) \times N25 10L	2.86	15.7	15.2	3.9	2.5	0.69	156	63	93.7	13.6	244.3
W22(IA) \times Oh43 10L	4.09	16.0	15.9	3.9	2.6	0.67	147	52	92.7	13.3	236.0
Mean	3.22	16.0	15.0	3.9	2.5	0.66	152	58	93.2	13.2	235.8
W22(WI) \times B55 10L	3.15	16.2	15.5	3.8	2.5	0.61	157	64	93.7	14.1	216.0
W22(WI) \times CI187-2 10L	2.36	15.8	15.4	3.8	2.6	0.59	158	63	96.2	16.3	212.0
W22(WI) \times M14 10L	2.88	17.2	15.8	3.8	2.6	0.61	151	59	95.0	17.9	194.0
W22(WI) \times N25 10L	2.68	15.9	14.8	3.7	2.4	0.65	156	59	94.4	14.6	229.7
W22(WI) \times Oh43 10L	3.03	16.1	15.1	3.7	2.5	0.62	146	56	95.1	15.8	198.3
Mean	2.82	16.2	15.3	3.8	2.5	0.62	154	60	94.9	15.7	210.0
W22 <i>R-scm2</i> \times B55 10L	3.40	15.6	15.6	3.7	2.5	0.59	150	61	92.2	12.1	225.7
W22 <i>R-scm2</i> \times CI187-2 10L	2.64	16.1	15.4	3.7	2.5	0.59	153	64	95.0	15.3	214.3
W22 <i>R-scm2</i> \times M14 10L	2.84	16.7	15.0	3.7	2.4	0.63	145	59	94.0	14.8	210.0
W22 <i>R-scm2</i> \times N25 10L	3.16	16.0	14.8	3.7	2.4	0.67	152	60	93.7	13.0	234.0
W22 <i>R-scm2</i> \times Oh43 10L	3.34	15.7	15.3	3.8	2.5	0.67	145	57	92.9	14.8	213.7
Mean	3.08	16.0	15.2	3.7	2.5	0.63	149	60	93.6	14.0	219.5
LSD (0.05)‡	0.74	0.9	1.6	0.3	0.1	0.11	13	9	1.8	2.6	20.0
LSD (0.05)§	0.27	0.4	0.7	0.1	0.04	0.05	6	4	0.8	1.1	8.8

† Values are averages for 1 yr.

‡ LSD for comparing individual hybrid means.

§ LSD for comparing W22 strain means.

pected to perform identically. For yield, the hybrid W22(WI) × W22 *R-scm2* was not significantly different from either of the other two hybrids or from the W22 strains per se. Hybrid W22(IA) × W22 *R-scm2* was significantly higher yielding than all the W22 strains, while the hybrid W22(IA) × W22(WI) was significantly higher yielding than both W22(IA) and W22(WI). The results for the other traits were similar to the results for yield.

These results were not entirely unexpected. Although all three strains originated at the University of Wisconsin, only W22(WI) and W22 *R-scm2* were maintained there, while W22(IA) was maintained by self pollination at Iowa State University for at least 25 generations. The evidence indicates that W22(IA) was higher yielding in hybrids than W22(WI) and W22 *R-scm2* (Table 2). This could be due to either W22(IA) having accumulated favorable alleles for yield during maintenance in Iowa that were not present in the other strains of W22 or W22(WI) and W22 *R-scm2* having accumulated unfavorable alleles during maintenance. The changes observed in W22(IA) seemingly were due to adaptation to the Iowa environment, although there was no direct evidence to support this hypothesis. Several studies have demonstrated that the routine maintenance of inbred lines of maize could lead to genetic changes (Bogenschutz and Russell, 1986; Higgs and Russell, 1968; and Busch and Russell, 1964).

Comparison of normal and 10L line performance Lines per se

All of the 10L substituted lines were lower yielding than their normal counterparts, except M14 10L and Oh43 10L, which were equal in yield to their normal counterparts (Table 1). The effect of the substituted 10L segment on line per se performance was obtained by comparing the performance of the 10L substituted lines with W22 *R-scm2*. Both CI187-2 10L and N25 10L were significantly lower yielding than W22 *R-scm2*, indicating that the 10L segment of these lines carry alleles detrimental to line per se performance in the W22 *R-scm2* background. B55 10L, M14 10L, and Oh43 10L were not significantly different from W22 *R-scm2* although they were significantly higher yielding than CI187-2 10L and N25 10L.

There were no significant differences between the substituted lines and W22 *R-scm2* for ear length and ear diameter. The substituted lines had larger cob diameters, except for N25 10L, which was smaller, although the differences were generally too small to be of practical significance. CI187-2 10L had fewer kernel rows, shallower kernel depth, smaller kernel size, and was 3 d later silking than W22 *R-scm2*. Kernel-row number, kernel depth, and kernel weight are all correlated with yield and may explain why CI187-2 10L was the lowest yielding line in the study. M14 10L had more kernel rows and smaller kernel size than W22 *R-scm2*. Four (B55 10L, M14 10L, N25 10L, and Oh43 10L) of the five lines had significantly lower ear height and Oh43 10L had significantly lower plant height, indicating that the 10L segment carries alleles for lower plant and ear height. M14 10L averaged five more tassel branches, and Oh43 10L was 36 g less for kernel weight than W22 *R-scm2*, suggesting that these lines carry major alleles on the 10L chromosome arm for these traits. The effects of the 10L chromosome segment were positive or negative, depending upon the inbred line that contributed the segment and the trait measured.

Comparisons of substituted lines with W22 *R-scm2* did not show a pattern of differences. However, M14 10L did show positive effects for kernel-row number, ear length, and tassel-branch number. CI187-2 10L generally showed negative effects for yield, kernel-row number, kernel depth, ear height, and days-to-silk. Overall, the 10L segment of M14 was most likely to show positive effects and CI187-2 was most likely to show negative effects with regard to maize improvement. These results generally agreed with those of Robertson et al. (1981), although there were some differences in the effects of the substituted segment, because their comparisons were made with W22(IA).

Hybrids

Significant MP heterosis was observed for most traits in the hybrids of the normal lines with the W22 strains (data not shown). As expected, all MP heterosis values were in the favorable direction. The negative estimates of MP heterosis for days-to-silk were expected

Table 3. Midparent heterosis values for the crosses of the W22 strains and the crosses of the W22 *R-scm2* with the five 10L substituted lines.

Genotype	Grain yield Mg ha ⁻¹	Kernel rows no.	Ear length cm	Diameter		Kernel depth cm	Height		Days to silk no.	Tassel branches no.	Kernel weight g
				Ear	Cob		Plant	Ear			
W22(IA) × W22 (WI)	0.92**	0.8*	0.9	0.1	0.1**	0.06	16	6	-1.5	2.5*	8.3
W22(IA) × W22 <i>R-scm2</i>	0.96**	0.8*	1.6*	0.2*	0.2**	0.05	15**	11**	-0.9	3.2**	-9.8
W22(WI) × W22 <i>R-scm2</i>	0.43	0.4	0.5	0.1	0.1**	0.02	1	3	-0.9	5.0**	-1.8
Mean	0.77**	0.6**	1.0*	0.1*	0.1**	0.04	10**	6**	-1.1*	3.5**	-1.1
W22 <i>R-scm2</i> × B55 10L	0.74*	0.4	1.5*	0.2*	0.1**	0.05	5.0	3.9	-1.3	2.3*	2.7
W22 <i>R-scm2</i> × CI187-2 10L	0.80*	1.0*	1.7*	0.2*	0.0	0.06	4.9	4.8	-0.6	5.3**	-7.3
W22 <i>R-scm2</i> × M14 10L	0.36	0.1	0.3	0.1	-0.1**	0.07	1.4	1.2	-0.7	1.6	-2.5
W22 <i>R-scm2</i> × N25 10L	1.06**	0.7	1.2	0.2*	0.1**	0.09	8.4	4.7	-1.0	2.3*	-0.8
W22 <i>R-scm2</i> × 10 Oh43 10L	0.67*	0.3	0.9	0.2*	0.1**	0.09	8.0	4.8	-0.9	4.0**	5.7
Mean	0.73**	0.5**	1.1**	0.2**	0.0	0.07**	5.5**	3.9*	-0.9**	3.1**	-0.5
SE(±)†	0.32	0.40	0.69	0.11	0.04	0.05	5.5	3.9	0.8	1.1	8.7
SE(±)‡	0.14	0.18	0.31	0.05	0.02	0.02	2.4	1.8	0.4	0.5	3.9
SE(±)§	0.19	0.23	0.40	0.06	0.02	0.03	3	2	0.5	0.6	5.0

*** Significant at the 0.05 and 0.01 probability levels, respectively.

† Standard error of individual hybrid means.

‡ Standard error of the mean over the five lines for each of the W22 strains.

§ Standard error of the mean of the three W22 strain crosses.

because early flowering is dominant in maize (Hallauer and Miranda, 1981).

The MP heterosis values of crosses to the normal lines were similar in magnitude for the three strains of W22. Although strain crosses demonstrated that W22(IA) was genetically different from W22(WI) and W22 *R-scm2*, the differences were not detected in the crosses to the normal lines. This, however, cannot be interpreted as evidence that W22(IA) is genetically similar to the other two W22 strains because of the masking effects of crossing to the normal lines. Busch and Russell (1964) discuss how tester lines may mask genetic alterations in strains of inbred lines.

Crosses of B55 10L, M14 10L, and Oh43 10L to W22(IA) were significantly higher yielding than W22(IA), suggesting the 10L segments of these lines carry alleles for yield not present in W22(IA) (Table 2). Crosses of CI187-2 10L and N25 10L to W22(IA) were approximately equal in yield to W22(IA), corresponding to their per se performance. The positive effect of the M14 10L segment on kernel-row number and tassel-branch number was also observed in hybrids with W22(IA). The Oh43 10L segment contributed significantly longer ears and the B55 10L segment contributed earlier flowering to hybrids with W22(IA). Crosses of the 10L substituted lines to W22(IA) were significantly higher yielding than the respective 10L substituted lines per se.

In crosses with W22(WI), only the B55 10L segment produced a significantly higher yielding hybrid than W22(WI) per se. The M14 10L segment produced a hybrid with significantly higher kernel-row number and the N25 10L segment contributed to significantly higher kernel weight. In no instance did a 10L substituted line produce a hybrid with W22(WI) that was inferior to W22(WI) per se. All traits of the 10L substituted line \times W22(WI) hybrids were either equal to or superior to the performance of the corresponding 10L substituted line.

Robertson et al. (1981) emphasized that considerable caution is needed in interpreting the results of the hybrids with W22(IA) and W22(WI) because the 10L substituted lines were in the background of W22 *R-scm2*. Results from our study suggest that much of the heterosis observed in the 10L substituted lines \times W22(IA) crosses may be due to the heterosis observed in the cross of W22(IA) \times W22 *R-scm2*.

In crosses with W22 *R-scm2*, only the two hybrids with B55 10L and Oh43 10L were significantly higher yielding than W22 *R-scm2* per se. Only two other 10L

substituted lines (M14 10L and CI187-2 10L) crossed with W22 *R-scm2* were significantly different from W22 *R-scm2* per se for the remaining 10 traits. The M14 10L \times W22 *R-scm2* hybrid had significantly more kernel rows than W22 *R-scm2* per se and significantly fewer kernel rows than M14 10L per se, indicating predominantly additive gene action for this trait. In contrast, CI187-2 10L \times W22 *R-scm2* had significantly more tassel branches than both CI187-2 10L and W22 *R-scm2*, indicating that the CI187-2 10L segment is carrying dominant genes for increased tassel-branch number. Other than the M14 10L line for kernel-row number, the 10L substituted lines \times W22 *R-scm2* hybrids were generally equal to or superior to the performance of the corresponding 10L substituted line.

Perhaps the best way of comparing the effects of the substituted chromosome segment is to examine MP heterosis values for the W22 *R-scm2* \times 10L substituted line hybrids. Use of MP heterosis values allows two important comparisons to be made: (i) a detection of whether there were significant heterotic effects attributable to the segment, by testing the null hypothesis that the MP heterosis was equal to zero; and (ii) a comparison of the relative size of the heterotic effects for the different segments. The MP heterosis values for the crosses of W22 *R-scm2* with the 10L substituted lines are shown in Table 3. MP heterosis values are not shown for the crosses involving W22(IA) and W22(WI) because the substituted lines are not in the background of these lines and the heterotic effects observed cannot be attributed solely to the substituted chromosome segment.

Significant MP heterosis for grain yield was observed for crosses of B55 10L, CI187-2 10L, N25 10L, and Oh43 10L to W22 *R-scm2*. The heterotic effect of N25 10L \times W22 *R-scm2* was the largest, although the effect was not significantly different from crosses of B55 10L, CI187-2, and Oh43 10L to W22 *R-scm2*. A significant heterotic effect for the M14 10L \times W22 *R-scm2* hybrid was not observed for grain yield. Generally, the four hybrids with significant heterotic effects for grain yield (i.e., B55 10L, CI187-2 10L, N25 10L, and Oh43 10L) also had significant heterotic effects for many of the same yield component traits. We do not consider the overall lack of heterotic effects for many of the yield component traits to be unusual because many of these traits are controlled by loci with alleles in the additive to partial dominance range (Hallauer and Miranda, 1981); therefore, heterotic effects

Table 4. Percentage of total midparent heterosis observed in the normal line \times W22 *R-scm2* hybrids accounted for in the 10L substituted line \times W22 *R-scm2* hybrids.

Genotype	Grain yield Mg ha ⁻¹	Kernel rows no.	Ear length	Diameter		Kernel depth cm	Height		Days to silk	Tassel branches no.	Kernel weight g
				Ear	Cob		Plant	Ear			
W22 <i>R-scm2</i> \times B55 10L	15.5	88.9†‡	32.0	25.0	33.3	20.4‡	11.1‡	14.5‡	23.4‡	31.5	4.2‡
W22 <i>R-scm2</i> \times CI187-2 10L	15.8	52.8	28.2	18.8	0.0‡	22.8‡	7.9‡	11.8‡	7.8‡	115.2	-15.8‡
W22 <i>R-scm2</i> \times M14 10L	9.4‡	5.6‡	4.9‡	16.7‡	-66.7	28.3‡	2.9‡	3.6‡	17.1‡	24.8‡	-11.6‡
W22 <i>R-scm2</i> \times N25 10L	20.8	77.8‡	27.7‡	27.3	16.7	62.1‡	16.0‡	18.7‡	19.6‡	24.3	-1.7‡
W22 <i>R-scm2</i> \times Oh43 10L	14.3	22.2‡	16.7‡	30.8	33.3	34.0‡	15.0‡	23.2‡	14.5‡	63.7	10.2‡
Mean	15.2	49.4	21.9	23.7	3.3‡	33.5	10.6	14.4	16.5	51.9	-3.0‡

† MP heterosis was not significant in the normal line \times W22 *R-scm2* hybrid.

‡ MP heterosis was not significant in the 10L substituted line \times W22 *R-scm2* hybrid.

were not expected or were difficult to detect from such a small segment of the genome.

The heterotic effects for cob diameter were significant for four of the five substituted lines, but they were too small to be of practical importance. Significant heterotic effects for the M14 10L \times W22 *R-scm2* hybrid were not observed for the plant and ear traits (ignoring cob diameter). The comparison of M14 10L \times W22 *R-scm2* hybrid data with the parental data indicated the possibility of additive gene action for kernel-row number, although definite conclusions cannot be drawn for the other traits. The possibility exists that the data were too imprecise to detect significant heterotic effects for M14 10L \times W22 *R-scm2*. The B55 10L \times W22 *R-scm2* hybrid showed significant heterotic effects for ear length, ear diameter, and tassel-branch number. The heterotic effects for CI187-2 10L \times W22 *R-scm2* were significant for kernel-row number, ear length, ear diameter, and tassel-branch number. The large positive effect of CI187-2 10L segment on tassel-branch number was unexpected because there was no related effect observed for CI187-2 10L per se. In contrast, M14 10L per se exhibited a large positive effect for tassel-branch number, but an effect was not detected in the hybrid with W22 *R-scm2*. There were significant heterotic effects for ear diameter and tassel-branch number for the N25 10L and Oh43 10L hybrids.

The absence of a heterotic effect does not preclude the possibility that a particular segment carries either favorable or unfavorable alleles for a trait. Five distinct explanations exist for the absence of a heterotic response: (i) If the effects of the alleles on a chromosome segment were additive, then a significant heterotic effect would not be expected. Additive gene action could be detected by a hybrid being significantly larger than one parent and significantly smaller than the other parent. (ii) The substituted segment could be allelically identical to W22 *R-scm2*. In this case, the hybrid performance would be expected to be equal to W22 *R-scm2*. (iii) Heterosis in the two allele case requires directional dominance (Falconer, 1981). If there were some loci on the 10L chromosome segment that were dominant for the favorable allele and some that were dominant for the unfavorable allele, there could be cancellation of effects resulting in no heterosis being observed. (iv) If the genes on the 10L chromosome segment were in the partial dominance range and were few in number, there may not have been enough precision in the experiment to detect a significant heterotic effect; (v) There could be cancellation of positive and negative epistatic effects, thus diminishing the amount of heterosis observed. Therefore, one could not prove whether the substituted segment carries favorable or unfavorable alleles for a trait; it could only be demonstrated that the segment has an effect.

The percentage of total MP heterosis attributed to the 10L segment in crosses with W22 *R-scm2* is shown in Table 4. B55 10L crossed to W22(IA) and W22(WI) had larger heterotic effects for kernel-row number than the corresponding crosses involving B55 (data not shown). This indicates the possibility that more of the

genome was contributing to the heterotic effects for kernel-row number than just the 10L segment. That more than the 10L segment might be involved in heterosis is not surprising for crosses with W22(IA) because the W22 *R-scm2* \times W22(IA) hybrid showed significant midparent heterosis for most traits (Table 3). Except for tassel-branch number, in all instances where the percentage of total heterosis accounted for by the W22 *R-scm2* \times 10L substituted line hybrids was greater than 100, the heterotic effects were not significantly different from zero in the normal line \times W22 *R-scm2* hybrids. The 10L segment accounted for 9.4 to 20.8% of the total heterosis observed for yield for an average of 15.2% in crosses to W22 *R-scm2*. For the plant and ear traits, the percentage of total heterosis ranged from -66.7 to 115.2%.

For those situations where the substituted segments made positive contributions toward the heterosis of the hybrid lines, the portion of the total heterotic response that could be attributed to the 10L segment varied among traits and among hybrids (Table 4). For any given trait, there was considerable variation among hybrids for the total contribution to heterosis that could be attributed to the 10L segment. This was probably due to variation in the level of dominance, directional dominance, and epistatic interactions that may exist between 10L loci for the particular trait and loci elsewhere in the genome. Because each hybrid has a unique genotype, these factors are expected to result in the variable results observed.

The results reported here establish the feasibility of studying discrete chromosome segments from inbreds for their contribution to the performance of the inbred per se and to ascertain the contribution of such segments in hybrid combinations. Such studies could be used to identify blocks of genes that might be useful for improving inbreds and their hybrid progeny. As more segments are analyzed it may be possible in the future to begin to combine different regions with a goal of creating superior inbreds and hybrids.

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